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THE INHERITANCE OF COLOR IN SHORT-HORN CATTLE

A STUDY IN SOMATIC BLENDS ACCOMPANYING GAMETIC SEGREGATION AND INTRA-ZYGOTIC INHIBITION AND REACTION

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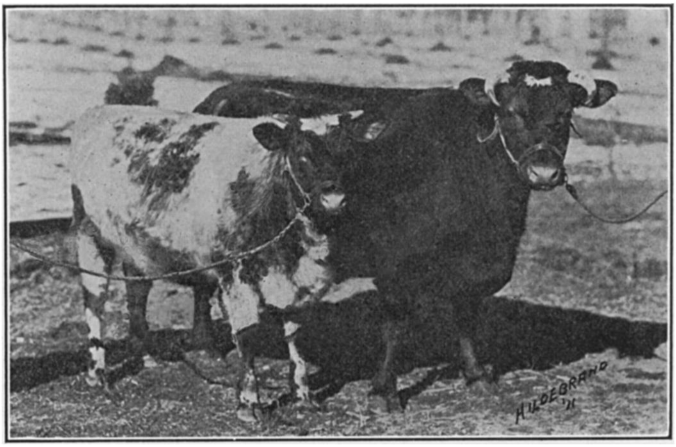
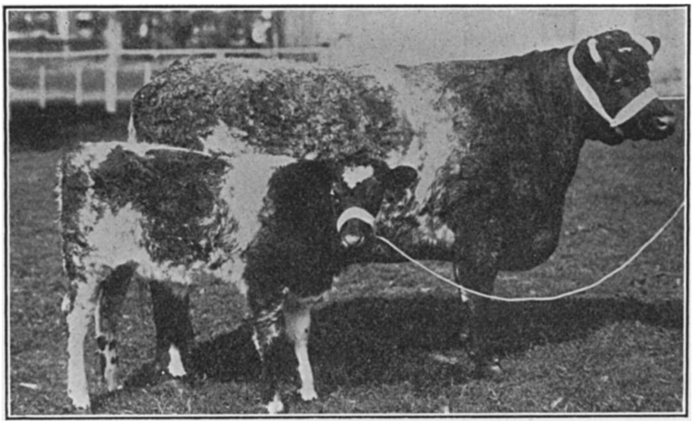
THE men who made the breed of Shorthorn cattle were in many respects the most skillful breeders of domestic animals. They had many rich and varied inheritance lines to draw upon, and in developing the breed they had high ideals of real excellence, largely ignoring the superficial quality of color. A consequence of this neglect of color is that the great breed of Shorthorn cattle is mongrel in this respect, ranging as follows: Solid red—varying from the richest dark to a light yellowish; spotted red-and-white; red-roan; and white—besides many intergrades and combinations of these shades and patterns. It is the prevailing experience among Shorthorn breeders that the color of the calf can not be accurately predicted before its birth. Reflecting this experience, Mr. B. O. Cowan, of the American Shorthorn Breeders' Association, writes:

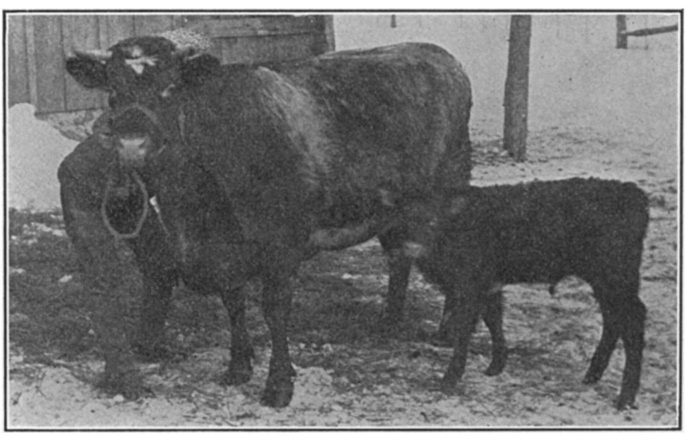
Owing to the fact that Shorthorns are of mixed colors, you can not with absolute certainty, before birth, tell what will be the color of the



Cinderella and Calf.



Mautalini 17th and Calf.



Pleasant Valley Bud and Calf.

Courtesy of Thos. Stanton, Wheaton, Ill.

COW—CINDERELLA. *Red.*

(White star on forehead.)

Dam—Clara. *Red.*
Dam's Dam—Carrie. *Red.*
Dam's Sire—Prince Gloster. *Red.*
Sire—Scottish Minstrel. *Dark Roan.*
Sire's Dam—Imp. Mistletoe 20th. *Roan.*
Sire's Sire—Imp. Collynie Mint. *Roan.*

CALF—CINDERELLA 2D. *Roan.*

Dam—Cinderella. *Red.*
Dam's Dam—Clara. *Red.*
Dam's Sire—Scottish Minstrel. *Dark Roan.*
Sire—Prince Imperial. *Light Roan.*
Sire's Dam—Imp. Helen 21st. *Light Roan.*
Sire's Sire—Prince. *Red.*

Courtesy of Geo. M. Rommel, Bureau of Animal Industry, Washington, D. C.

COW—MAUTALINI 17TH. *Roan.*

(A champion Argentine (S. A.) cow.)
Dam—Mautalini 8th. *Red.*
Dam's Dam—Mautalini 3d. *Red.*
Dam's Sire—Farrier. *Roan.*
Sire—Conqueror's Crown. *Roan.*
Sire's Dam—Missie 157. *Roan.*
Sire's Sire—Bapton Conqueror. *Roan.*

CALF. *Roan.*

Dam—Mautalini 17th. *Roan.*
Dam's Dam—Mautalini 8th. *Red.*
Dam's Sire—Conqueror's Crown. *Roan.*
Sire—True Blue. *Red and White.*
Sire's Dam—Twin Princess 10th. *Red and White.*
Sire's Sire—Bapton Champion. *Roan.*

Courtesy of F. W. Harding, Waukesha, Wis.

COW—PLEASANT VALLEY BUD. *Roan.*

Dam—Rosebud 11th. *Red.*
Dam's Dam—Rosedale. *Red.*
Dam's Sire—John Bruce. *Roan.*
Sire—Ben Lomond (Imp.). *Red.*
Sire's Dam—Beauty 13th. *Roan.*
Sire's Sire—Count St. Clair. *Roan.*

CALF. *Red.*

Dam—Pleasant Valley Bud. *Roan.*
Dam's Dam—Rosebud 11th. *Red.*
Dam's Sire—Ben Lomond (Imp.). *Red.*
Sire—Waverley. *Roan.*
Sire's Dam—Valley Gem. *Red.*
Sire's Sire—Mildred's Royal. *Roan.*

FIG. 1.

calves. There are a great many instances of red cows bred to white bulls producing red calves, in some instances white calves, and in other instances roans. In some herds in the United States where the breeders have used nothing but red for thirty or forty years it is very rare that they have any calves excepting reds; but even among these occasionally a calf is dropped that is either a roan or a red with some white marks —this is the influence of the blood of ancestors many generations back.

Mr. Spangler, of Sullivan County, Mo., reports the following to the *Breeders' Gazette* of February 17, 1909:

My bull is white, but his sire and dam are both roan. The results are as follows: Since September first there have been fifty-five calves dropped to his service, of these forty-one are roan, nine red, four red-and-white, and one white. Twenty-six are bulls and twenty-nine heifers. The cow that dropped the white calf is herself a roan . . . the rest of the cows are red.

Robert Bruce, of County Dublin, Ireland, tabulated the color matings and color progeny of Shorthorns bred by Amos Cruickshank[1] at Sittyton. This he reports to the *Breeders' Gazette* of November 25, 1908, as follows:

TABLE I

	Color of Offspring				
Color of Matings	Red	Rd. & Wh.	Roan	White	Total
Red mated with red	133	12	34	1	180
Red mated with red and white	31	11	6	0	48
Red mated with roan	278	25	265	0	568
Red mated with white	1	0	41	4	46
Red and white mated with red and white	0	2	0	1	3
Red and white mated with roan	22	22	40	2	86
Red and white mated with white	0	1	1	1	3
Roan mated with roan	56	10	183	60	309
Roan mated with white	0	0	12	12	24
White mated with white	0	0	1	2	3
	521	83	583	83	1,270

Professor E. N. Wentworth, of Ames, Ia., supplies the following tabulation from random pedigrees:

[1] Amos Cruickshank, of Sittyton (1808–1895), the most distinguished breeder of Shorthorns, and one of the most skillful breeders of domestic animals.

TABLE II

Offspring	Parentage
127 whites	43 from white by white matings.
	1 from red by red matings.
	83 from roan by roan matings.
645 roans	207 from roan by roan matings.
	122 from red by roan matings.
	8 from red by red matings.
	172 from white by red and white matings.
	136 from red by red and white matings.
892 reds	81 from roan by roan matings.
	439 from red by red matings.
	52 from red by red and white matings.
	320 from red by roan matings.
Total 1,664 animals	

The following table (No. III) records some matings, selected almost at random from the Shorthorn Herd Book, detailing the color of dam, sire and offspring, the last animal of this table, the *roan* cow Dorothea (Vol. 45, p. 645), herself a roan from two red parents, produced six calves: The first a *roan* Trout Creek Beauty, by the *red-and-white* Klondike of Baltimore; the second the *red-and-white* Lord Strathearn by the *red* Strathearn Oakland; the third the *red* Dorothea's Knight by the *red* Red Knight; the fourth the *white* Bapton Favorite by the *roan* Bapton Ensign; the fifth the *roan* Dorothea Second by the *red* March King, and the sixth the *red-and-white* Dorothea Third by the *red* March King. It is interesting to note that one cow can produce calves of each color characteristic of the race.

In color pattern the red-and-white and the roan-and-white Shorthorns are quite similar to all other breeds of cattle possessing broken patterns—that is to say, there is a tendency toward a white belt at the front flank, a slightly more pronounced one at the rear flank and a white underline. It is known that Angus cattle which are generally black sometimes possess white patches, generally within the line of the rear flank belt. A white Shorthorn bred to a black Angus or Galloway will produce a blue-roan calf, or when bred to a white-faced, roan-bodied

TABLE III

Dam			Sire			Offspring		
Grenedine	*White*	×	Wild Eyes	*Roan*	=	Grenedine 2nd		*Roan*
Jordan	*White*	×	The Baron	*Red and White*	=	Jewess		*Roan*
Jordan	*White*	×	Maple 4th	*Roan*	=	Truey		*Roan*
Farnside	*Roan*	×	Phoebus	*Roan*	=	Nuthall Prince		*White*
Farnside	*Roan*	×	Jeweller	*Roan*	=	Fair Maid		*Roan*
Farnside	*Roan*	×	Jeweller	*Roan*	=	Crown Prince		*Roan*
Farnside	*Roan*	×	Prince	*Roan*	=	Fanny Fern		*Roan*
Fawn	*Red and White*	×	Sir A. Windsor	*Red*	=	Ferculus		*Red and White*
Fawn	*Red and White*	×	Sir A. Windsor	*Red*	=	Friar		*Roan*
Repose	*Red and White*	×	4th Kent Oxford	*Light Roan*	=	Knightly Oxford		*Red and White*
Repose	*Red and White*	×	Red Cross Knight	*Red*	=	Red Cross Knight's Repose		*Red and White*
Repose	*Red and White*	×	Red Cross Knight	*Red*	=	Ruby		*Red and White*
Susan Gwynne	*Roan*	×	Sir Samuel	*Roan*	=	Soral		*Red*
Susan Gwynne	*Roan*	×	Conqueror	*White*	=	Lady Gwynne	Twins	*White*
						Lord Gwynne	Twins	*Roan*
Susan Gwynne	*Roan*	×	First Fruit	*Roan*	=	Earl Gwynne		*Roan*
Galaxy	*White*	×	Esca	*Roan*	=	Gaiety		*White*
Bapton Pearl	*Roan*	×	Auguston	*Roan*	=	Bapton Diamond		*Roan*
Bapton Pearl	*Roan*	×	Bapton Sultan	*Roan*	=	White Hall Sultan		*White*
Augusta Countess	*White*	×	Bapton Javelin	*Red*	=	Auguston		*Roan*
Moon Daisy	*Roan*	×	Capt. of the Guard	*Red*	=	Bapton Sultan		*Roan*
Victoria-of-Hill Farm 5th	*Roan*	×	Lavender Lad	*Red*	=	Victoria-of-Hill Farm 8th		*Roan*
Victoria-of-Hill Farm 8th	*Roan*	×	Robin Adair	*Red*	=	Proud Robin		*Red and Roan*
Victoria-of-Hill Farm 8th	*Roan*	×	Robin Adair	*Red*	=	White Hall Victor		*Red*
Victoria-of-Hill Farm 8th	*Roan*	×	White Hall Sultan	*White*	=	Glen Brook Sultan		*White*
Victoria-of-Hill Farm 8th	*Roan*	×	Victor Missie	*Red*	=	Victor Missie's Victoria		*Roan*
Sousie's Maid	*Roan*	×	Sheriff Hutton	*Roan*	=	Lady Jane Hutton		*Red*
Lady Jane Hutton	*Red*	×	Crimson Chief	*Red*	=	Dorothea		*Roan*

Hereford will produce a white-faced, roan-bodied or red-bodied calf. It is also known that a black Angus bred to a white-faced, red-bodied Hereford will produce a calf with a white face and a black body. A roan Shorthorn

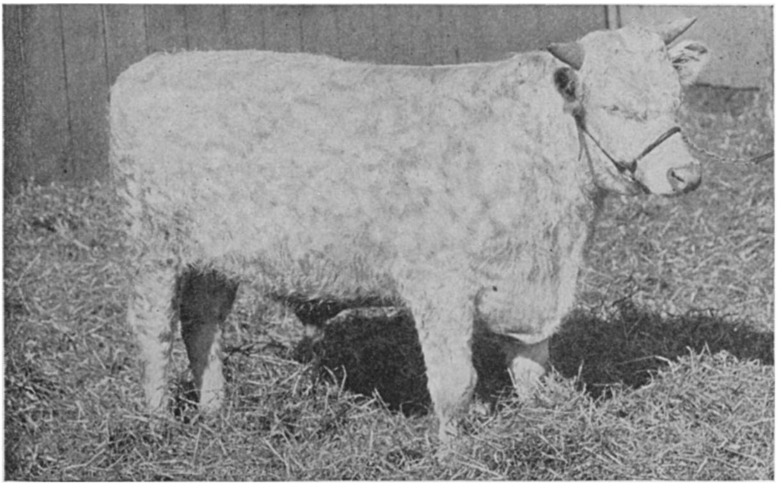


FIG. 2. BROODHOOKS CHIEF.

BROADHOOKS CHIEF 348176. *White.*

Courtesy of F. W. Harding, Waukesha, Wis.

Dam—Broadhooks Rose 101234. *Roan.*
Dam's Dam—Imp. Roan Rose 75966. *Roan.*
Dam's Sire—Rustic Chief 236800. *Roan.*

Sire—Royal Fancy 93217. *Roan.*
Sire's Dam—Sensation 7th. *Red.*
Sire's Sire—Prince of Fashion 64587. *Red.*

mated with a black Angus or Galloway will sometimes produce a black and sometimes a blue-roan calf; as instances of the former, Mr. Ralph B. Goodhue, of Donnelly, Minn., writes:

I have had a few animals cross-bred between Angus and Shorthorn and in every instance have the offspring been black, sire and dams pure bred animals. I have bred 31/32 Holstein cows to red Shorthorn bulls and about 65 per cent. have been red-and-white, the rest being black-and-white, more black than white in markings. In breeding grade Shorthorn cows to pure bred Holstein bulls, have got black and white offspring. In the Hereford-Shorthorn, the red Shorthorn bred with the Hereford will most always give a mottled face on the offspring. The roan Shorthorn cows bred to Hereford bulls will give either a calf looking like a Hereford or a roan calf with clear white face.

Professor Wentworth, previously referred to, writes:

In regard to color coats in cattle hybrids, I can give you a few cases from my own experience.

We had three Holstein cows at home, two of them carrying a predominance of black, the other a predominance of white. As we had no Holstein bull on three successive years, they were bred to Shorthorn bulls. The first year when bred to a roan one of the calves came a blue gray. This calf was from the cow with the greatest amount of black. The others showed the pattern markings of their mothers. The second year they were bred to a deep red Shorthorn bull (all of the animals mentioned pure breds) and the color pattern showed no trace whatsoever of the Shorthorn parentage. The third year they were bred to a red and white bull. In the case of the lightest Holstein cow there seemed to be some tinge of red on the ends of the hair in the black pattern; however, at a distance it showed the same color.

I have seen Jersey-Holstein crosses usually partaking of the Holstein pattern with, perhaps, a slight admixture of dun color on the tips of the hair on the black markings.

I have seen Angus crossed on Jersey showing simply the black polled character, although in a few cases the extremities showed a slight tendency towards dun or fawn.

I have seen Angus crossed with Holstein and have seen both pure black and black-and-white cows. The instances which I have in mind are about twenty showing pure black and six or seven showing the black-and-white. However, these figures are simply a question of memory and might easily be modified. The case in question is that of a man with a Holstein herd who was forced to breed to an Angus bull one year.

Out at the dairy farm we have a Shorthorn cow, roan in color but a grade, which was bred to our Holstein bull, a half brother of Colanta 4th's Johanna. The calf is roan in color.

We also have some Arkansas backwoods cows; they are variegated in color pattern, showing red, dun, yellow, white, brindle and various other markings. A Holstein bull when bred to one of these produced a nearly pure black heifer. The black seemed to be rather tinged with brown at the ends of the hair, but the udder showed a white color. . . . A roan Shorthorn bull bred to a Hereford cow will quite frequently give a roan body with white Hereford markings. A red Shorthorn bull crossed with the Hereford cow is apt to increase the red splotches on the white markings of the Hereford.

Mr. P. G. Ross, of the famous Maxwalton Farm, Mansfield, O., relates his experience, throwing his observations into approximate percentages, as follows:

The color of the offspring of white Shorthorns depends largely on the ancestors, as about 50 per cent. of a bull's calves will have the color of

his dam and her ancestors. . . . We have used white on white and often had roan calves and in one instance had a red calf, but about 75 per cent. are white.

We have had considerable experience in crossing the Shorthorn on Angus. This we consider the best cross and the offspring is generally better than either of the parents. When crossing red and black the offspring are generally 75 per cent. blacks and even the second cross will not bring 50 per cent. reds; when crossing roan and black, about 50 per cent. will be blue-roans, 10 per cent. red-roans, 10 per cent. reds and 30 per cent. blacks. The Galloway color is much stronger than the Angus, consequently more dark calves will be expected. The Hereford cross is very strong as far as the white face is concerned and about 95 per cent. of white heads can be expected but the red of the body is easily blended into a roan and about 95 per cent. roan calves can be expected by a white bull, and at least 75 per cent. by roan bull, on Hereford cows.

The black of the Holstein seems to be particularly strong and when crossed with red the offspring will be nearly black and will remain very predominant to the third and fourth cross; the broken color shows itself but very little. . . . On the other hand, Holsteins take the roan color very readily and when crossed on white 95 per cent., and when crossed on roan 75 per cent. of the calves will be blue-roan. It is our experience that either the Holstein or the Hereford will take the roan color from a white or roan much oftener than from the red Shorthorn even if part of the red's ancestry were roans. The Red Polls and Devons seem to be very hard to blend into a roan and when crossed on a white not over 25 per cent. roans can be expected; the balance are red. This we do not consider strange as they have been bred red for so many generations. It would seem that the red color of the Shorthorn is not so strong as the roan when used in crossing, and in our opinion it is the most objectionable. . . . We believe that to maintain the standard we must exert judgment in crossing the best types and colors, as it is evident in both animals and plants that they must have fresh blood to prosper and this is seen much earlier in breeding the short-lived animals such as hogs, dogs, cats and rabbits. We feel that the Shorthorn has given a much better opportunity for crossing than any other breed of cattle as there is very little restriction as to standard color. The different color is, we feel, a very safe rule to go by in crossing and we are particularly opposed to using red on red no matter if the ancestors are desirable. We feel that white on red is the proper cross and roan is good to cross on anything.

The observed facts fit the following hypothesis so closely that it is presented as a further working basis in solving the problem of the prediction of the color and color pattern in Shorthorn cattle.

Hypothesis.—There are two groups of genetically independent sets of hairs intermingled to make up the Shorthorn color coat. One set is alternatively "positive white" (W) and red (R), in which the white is dominant and the red recessive; the other set is alternatively red (R) or "albinic white" (wr), in which the red is dominant and the white recessive. Dominant white is caused by a

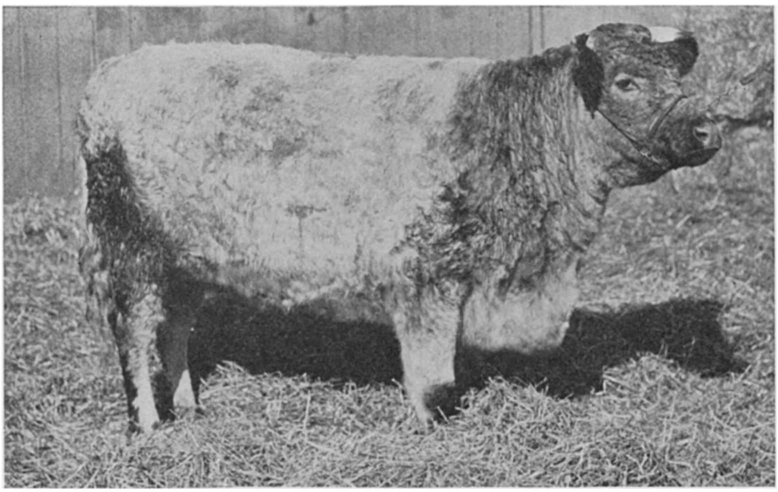


FIG. 3. ANOKA ACONITE 2D.

ANOKA ACONITE 2D 40311. *Roan.*

Courtesy of F. W. Harding, Waukesha, Wis.

Dam—Double Aconite 2d. Vol. 53, p. 563. *Red.*
Dam's Dam—Double Aconite. *Roan.*
Dam's Sire—Godoy 115575. *Red.*

Sire—Whitehall Marshall 209776. *Roan.*
Sire's Dam—Imp. Missie 167th. *Roan.*
Sire's Sire—Whitehall Sultan 163573. *White.*

specific antibody existing in the zygote in small quantities, retarding or inhibiting the ontogenesis of the determiner for pigmentation. The same body existing in larger quantities reacts with and destroys the determiner for pigmentation, causing recessive or albinic white.

The dominant white of the Shorthorn is doubtless derived from the Romano-British cattle, which it is generally conceded entered into the Shorthorn make-up, which element is to-day represented by the "Park Cattle." They

behave as dominant whites—*i. e.,* they themselves are white but sometimes throw red or black (not roan) calves. The recessive white doubtless came in with the Dutch flecked, the colored areas of which took the "differential coloring" because they lacked the positive graying factor; this recessive white must therefore be attributed to a strain of partial albinism. The spotted color pattern or coarse mosaic doubtless came in with the Dutch bulls of the eighteenth-century importation. The areas composing *Group One* are located about the two flank belts, the underline, the median line and the face and a fine network over the remainder of the body; those composing *Group Two* cover the neck, sides, back, hind quarters and legs in a network exclusive of the areas of Group One.

FACTORS CONSIDERED

W = Inhibitor of pigment formation.
w = Absence of such inhibitor.
R = Determiner for red pigmentation.
r = Absence of determiner for red pigmentation.

With reference to Set No. 1, or group-unit No. 1, individual cattle are gametically W_2r_2, W_wR_2 or w_2R_2. With reference to group-unit No. 2 they are w_2R_2, w_2R_r or w_2r_2. There are therefore involving these characters nine gametic and three somatic types of individuals, which types are set forth in the following table:

TABLE IV

	Gametic Composition Set 1	Gametic Composition Set 2	Somatic Aspect	Blood	Unit Purity Set 1	Unit Purity Set 2
1	w_2R_2	w_2R_2	Red	Pure	Duplex	Duplex
2	w_2R_2	w_2Rr	Red	Mongrel	Duplex	Simplex
3	w_2R_2	w_2r_2	Roan	Pure	Duplex	Nulliplex
4	WwR_2	w_2R_2	Roan	Mongrel	Simplex	Duplex
5	WwR_2	w_2Rr	Roan	Mongrel	Simplex	Simplex
6	WwR_2	w_2r_2	White	Mongrel	Simplex	Nulliplex
7	W_2r_2	w_2R_2	Roan	Pure	Duplex	Duplex
8	W_2r_2	w_2Rr	Roan	Mongrel	Duplex	Simplex
9	W_2r_2	w_2r_2	White	Pure	Duplex	Nulliplex

Roan in this table stands for any animal with red and white hairs interspersed, regardless of the proportion or pattern.

All of these theoretical types seem to occur except the roan of type 3, which phenomenon will be discussed further on in this paper.

With these nine theoretical types of individuals the following forty-five type matings are possible. (The numbers following the color designations refer to the above table describing the individuals somatically and gametically.)

These forty-five cases typify the behavior of two companion traits of opposing patency in their dominant phases, thus explaining the behavior of one type of apparent or somatic blend, which is in fact the resultant somatic effect of the lack of synchronism in the behavior of genetically independent units.

With these matings it is noted that the cases joined by an arrow (cases 8 and 9, 10 and 11, 13 and 14, 17 and 18, 19 and 20, 22 and 23, 32 and 33, 34 and 35, and 37 and 38) are reciprocal cases wherein the same parental elements enter and the same offspring are expected, but these parental elements are differently combined in each pair of parents—different somatic but identical gametic matings. These principles fit the previously observed facts as follows: As to the attempt to establish a race of Red Shorthorns, the above mating No. 30 (a red by red) expects 25 per cent. roan offspring and amply accounts for the occurrence of roans in such a cross. This phenomenon is equally well accounted for by the simple hypothesis that red is dominant; some reds are simplex. It is known that breeders in attempting to eliminate white, spotted and roan from their stock simply destroyed the "off color" calf—the genotypic germ plasm that produced it being continued in the herd. There are, however, reds which will produce only reds, as in matings Nos. 6 and 15.

Mr. Spangler's white bull was produced by two roan parents; such color is expected from such a mating in one fourth of the offspring of matings Nos. 25, 26, 37; in three sixteenths of No. 28 and in one half of No. 34. His whiteness is of either type 6 or type 9 and consequently

TABLE V

	One Parent	2d Parent	Intermediate Calculations	Gametic and Somatic Composition of Offspring
1. Set 1.	(W_2r_2)	(W_2r_2)	$= 4\ W_2r_2$	$16\ W_2r_2w_2R_2$
Set 2.	(w_2R_2)	(w_2R_2)	$= 4\ w_2R_2$	Roan 7
Somatic effect	Roan 7	Roan 7		
2.	(W_2r_2)	(WwR_2)	$= 2\ W_2r_2 + 2\ WwR_2$	$8\ W_2r_2w_2R_2 + 8\ WwR_2w_2R_2$
	(w_2R_2)	(w_2R_2)	$= 4\ w_2R_2$	Roan 7 Roan 4
	Roan 7	Roan 4		
3.	(W_2r_2)	(w_2R_2)	$= 4\ WwR_2$	$16\ WwR_2w_2R_2$
	(w_2R_2)	(w_2R_2)	$= 4\ w_2R_2$	Roan 4
	Roan 7	Red 1		
4.	(WwR_2)	(WwR_2)	$= W_2r_2 + 2\ WwR_2 + w_2R_2$	$4\ W_2r_2w_2R_2 + 8\ WwR_2w_2R_2 + 4\ w_2R_2w_2R_2$
	(w_2R_2)	(w_2R_2)	$= 4\ w_2R_2$	Roan 7 Roan 4 Red 1
	Roan 4	Roan 4		
5.	(WwR_2)	(w_2R_2)	$= 2\ WwR_2 + 2\ w_2R_2$	$8\ WwR_2w_2R_2 + 8\ w_2R_2w_2R_2$
	(w_2R_2)	(w_2R_2)	$= 4\ w_2R_2$	Roan 4 Red 1
	Roan 4	Red 1		
6.	(w_2R_2)	(w_2R_2)	$= 4\ w_2R_2$	$16\ w_2R_2w_2R_2$
	(w_2R_2)	(w_2R_2)	$= 4\ w_2R_2$	Red 1
	Red 1	Red 1		
7.	(W_2r_2)	(W_2r_2)	$= 4\ W_2r_2$	$8\ W_2r_2w_2R_2 + 8\ W_2r_2w_2Rr$
	(w_2R_2)	(w_2Rr)	$= 2\ w_2R_2 + 2\ w_2Rr$	Roan 7 Roan 8
	Roan 7	Roan 8		

TABLE V (*continued*)

	One Parent	2d Parent	Intermediate Calculations	Gametic and Somatic Composition of Offspring
8.	(W_2r_2) (w_2R_2) Roan 7	(WwR_2) (w_2Rr) Roan 5	$= 2\ W_2r_2 + 2\ Wwr_2$ $= 2\ w_2R_2 + 2\ w_2R_2$	$4\ W_2r_2w_2R_2 + 4\ W_2r_2w_2Rr + 4\ WwR_2w_2R_2 + 4\ WwR_2w_2Rr$ Roan 7, Roan 8, Roan 4, Roan 5
9.	(WwR_2) (w_2R_2) Roan 4	(W_2r_2) (w_2Rr) Roan 8	$= 2\ W_2r_2 + 2\ WwR_2$ $= 2\ w_2R_2 + 2\ w_2Rr$	$4\ W_2r_2w_2R_2 + 4\ W_2r_2w_2R_2 + 4\ WwR_2w_2R_2 + 4\ WwR_2w_2Rr$ Roan 7, Roan 8, Roan 4, Roan 5
10.	(W_2r_2) (w_2R_2) Roan 7	(w_2R_2) (w_2Rr) Red 2	$= 4\ WwR_2$ $= 2\ w_2R_2 + 2\ w_2Rr$	$8\ WwR_2w_2R_2 + 8\ WwR_2w_2Rr$ Roan 4, Roan 5
11.	(w_2R_2) (w_2R_2) Red 1	(W_2r_2) (w_2Rr) Roan 8	$= 4\ WwR_2$ $= 2\ w_2R_2 + 2\ w_2Rr$	$8\ WwR_2w_2R_2 + 8\ WwR_2w_2Rr$ Roan 4, Roan 5
12.	(WwR_2) (w_2R_2) Roan 4	(WwR_2) (w_2Rr) Roan 5	$= W_2r_2 + 2\ WwR_2 + w_2R_2$ $= 2\ w_2R_2 + 2\ w_2Rr$	$2\ W_2r_2w_2R_2 + 2\ W_2r_2w_2Rr + 4\ WwR_2w_2R_2 + 4\ WwR_2w_2Rr$ Roan 7, Roan 8, Roan 4, Roan 5 $+ 2\ w_2R_2w_2R_2 + 2\ w_2R_2w_2Rr$ Red 1, Red 2
13.	(WwR_2) (w_2R_2) Roan 4	(w_2R_2) (w_2Rr) Red 2	$= 2\ WwR_2 + 2\ w_2R_2$ $= 2\ w_2R_2 + 2\ w_2Rr$	$4\ WwR_2w_2R_2 + 4\ WwR_2w_2Rr + 4\ w_2R_2w_2R_2 + 4\ w_2R_2w_2Rr$ Roan 4, Roan 5, Red 1, Red 2
14.	(w_2R_2) (w_2R_2) Red 1	(WwR_2) (w_2Rr) Roan 5	$= 2\ WwR_2 + 2\ w_2R_2$ $= 2\ w_2R_2 + 2\ w_2Rr$	$4\ WwR_2w_2R_2 + 4\ WwR_2w_2Rr + 4\ w_2R_2w_2R_2 + 4\ w_2R_2w_2Rr$ Roan 4, Roan 5, Red 1, Red 2
15.	(w_2R_2) (w_2R_2) Red 1	(w_2R_2) (w_2Rr) Red 2	$= 4\ w_2R_2$ $= 2\ w_2R_2 + 2\ w_2Rr$	$8\ w_2R_2w_2R_2 + 8\ w_2R_2w_2Rr$ Red 1, Red 2

TABLE V (*continued*)

	One Parent	2d Parent	Intermediate Calculations	Gametic and Somatic Composition of Offspring
16.	(W_2r_2) (w_2R_2) Roan 7	(W_2r_2) (w_2r_2) White 9	$= 4\ W_2r_2$ $= 4\ w_2Rr$	$16\ W_2r_2w_2Rr$ Roan 8
17.	(W_2r_2) (w_2R_2) Roan 7	(WwR_2) (w_2r_2) White 6	$= 2\ W_2r_2 + 2\ WwR_2$ $= 4\ w_2Rr$	$8\ W_2r_2w_2Rr + 8\ WwR_2w_2Rr$ Roan 8 Roan 5
18.	(WwR_2) (w_2R_2) Roan 4	(W_2r_2) (w_2r_2) White 9	$= 2\ W_2r_2 + 2\ WwR_2$ $= 4\ w_2Rr$	$8\ W_2r_2w_2Rr + 8\ WwR_2w_2Rr$ Roan 8 Roan 5
19.	(W_2r_2) (w_2R_2) Roan 7	(w_2R_2) (w_2r_2) Roan 3	$= 4\ WwR_2$ $= 4\ w_2Rr$	$16\ WwR_2w_2Rr$ Roan 5
20.	(w_2R_2) (w_2R_2) Red 1	(W_2r_2) (w_2r_2) White 9	$= 4\ WwR_2$ $= 4\ w_2Rr$	$16\ WwR_2w_2Rr$ Roan 5
21.	(WwR_2) (w_2R_2) Roan 4	(WwR_2) (w_2r_2) White 6	$= W_2r_2 + 2\ WwR_2 + W_2R_2$ $= 4\ w_2Rr$	$4\ W_2r_2w_2Rr + 8\ WwR_2w_2Rr + 4\ w_2R_2w_2Rr$ Roan 8 Roan 5 Red 2
22.	(WwR_2) (w_2R_2) Roan 4	(w_2R_2) (w_2r_2) Roan 3	$= 2\ WwR_2 + 2\ w_2R_2$ $= 4\ w_2Rr$	$8\ WwR_2w_2Rr + 8\ w_2R_2w_2Rr$ Roan 5 Red 2
23.	(w_2R_2) (w_2R_2) Red 1	(WwR_2) (w_2r_2) White 6	$= 2\ WwR_2 + 2\ w_2R_2$ $= 2\ w_2Rr$	$8\ WwR_2w_2Rr + 8\ w_2R_2w_2Rr$ Roan 5 Red 2

TABLE V (*continued*)

	One Parent	2d Parent	Intermediate Calculations	Gametic and Somatic Composition of Offspring
24.	(w_2R_2) (w_2R_2) Red 1	(w_2R_2) (w_2r_2) Roan 3	$= 4\ w_2R_2$ $= 4\ w_2Rr$	$16\ w_2R_2w_2Rr$ Red 2
25.	(W_2r_2) (w_2Rr) Roan 8	(W_2r_2) (w_2Rr) Roan 8	$= 4\ W_2r_2$ $= w_2R_2 + 2\ w_2Rr + w_2r_2$	$4\ W_2r_2w_2R_2 + 8\ W_2r_2w_2Rr + 4\ W_2r_2w_2r_2$ Roan 7, Roan 8, White 9
26.	(W_2r_2) (w_2Rr) Roan 8	(WwR_2) (w_2Rr) Roan 5	$= 2\ W_2r_2 + 2\ WwR_2$ $= w_2R_2 + 2\ w_2Rr + w_2r_2$	$2\ W_2r_2w_2R_2 + 4\ W_2r_2w_2Rr + 2\ W_2r_2w_2r_2 + 2\ WwR_2w_2R_2$ Roan 7, Roan 8, White 9, Roan 4 $+ 4\ WwR_2w_2Rr + 2\ WwR_2w_2r_2$ Roan 5, White 6
27.	(W_2r_2) (w_2Rr) Roan 8	(w_2R_2) (w_2Rr) Red 2	$= 4\ WwR_2$ $= w_2R_2 + 2\ w_2Rr + w_2r_2$	$4\ WwR_2w_2R_2 + 8\ WwR_2w_2Rr + 4\ WwR_2w_2r_2$ Roan 4, Roan 5, White 6
28.	(WwR_2) (w_2Rr) Roan 5	(WwR_2) (w_2Rr) Roan 5	$= W_2r_2 + 2\ WwR_2 + w_2R_2$ $= w_2R_2 + 2\ w_2Rr + w_2r_2$	$W_2r_2w_2R_2 + 2\ W_2r_2w_2Rr + W_2r_2w_2r_2 + 2\ WwR_2w_2R_2$ Roan 7, Roan 8, White 9, Roan 4 $+ 2\ WwR_2w_2r_2 + w_2R_2w_2R_2 + 2\ w_2R_2w_2Rr + w_2R_2w_2r_2$ White 6, Red 1, Red 2, Roan 3 $+ 4\ WwR_2w_2Rr$ Roan 5
29.	(WwR_2) (w_2Rr) Roan 5	(w_2R_2) (w_2Rr) Red 2	$= 2\ WwR_2 + 2\ w_2R_2$ $= w_2R_2 + 2\ w_2Rr + w_2r_2$	$2\ WwR_2w_2R_2 + 4\ WwR_2w_2Rr + 2\ WwR_2w_2r_2 + 2\ w_2R_2w_2R_2$ Roan 4, Roan 5, White 6, Red 1 $+ 4\ w_2R_2w_2Rr + 2\ w_2R_2w_2r_2$ Red 2, Roan 3
30.	(w_2R_2) (w_2Rr) Red 2	(w_2R_2) (w_2Rr) Red 2	$= 4\ w_2R_2$ $= w_2R_2 + 2\ w_2Rr + w_2r_2$	$4\ w_2R_2w_2R_2 + 8\ w_2R_2w_2Rr + 4\ w_2R_2w_2r_2$ Red 1, Red 2, Roan 3

TABLE V (*continued*)

	One Parent	2d Parent	Intermediate Calculations	Gametic and Somatic Composition of Offspring
31.	(W_2r_2) (w_2Rr) Roan 8	(W_2r_2) (w_2r_2) White 9	$= 4\ W_2r_2$ $= 2\ w_2Rr + 2\ w_2r_2$	$8\ W_2r_2w_2Rr + 8\ W_2r_2w_2r_2$ Roan 8, White 9
32.	(W_2r_2) (w_2Rr) Roan 8	(WwR_2) (w_2r_2) White 6	$= 2\ W_2r_2 + 2\ WwR_2$ $= 2\ w_2Rr + 2\ w_2r_2$	$4\ W_2r_2w_2Rr + 4\ W_2r_2w_2r_2 + 4\ WwR_2w_2Rr + 4\ WwR_2w_2r_2$ Roan 8, White 9, Roan 5, White 6
33.	(WwR_2) (w_2Rr) Roan 5	(W_2r_2) (w_2r_2) White 9	$= 2\ W_2r_2 + 2\ WwR_2$ $= 2\ w_2Rr + 2\ w_2r_2$	$4\ W_2r_2w_2Rr + 4\ W_2r_2w_2r_2 + 4\ WwR_2w_2Rr + 4\ WwR_2w_2r_2$ Roan 8, White 9, Roan 5, White 6
34.	(W_2r_2) (w_2Rr) Roan 8	(w_2R_2) (w_2r_2) Roan 3	$= 4\ WwR_2$ $= 2\ w_2Rr + 2\ w_2r_2$	$8\ WwR_2w_2Rr + 8\ WwR_2w_2r_2$ Roan 5, White 6
35.	(w_2R_2) (w_2Rr) Red 2	(W_2r_2) (w_2r_2) White 9	$= 4\ WwR_2$ $= 2\ w_2Rr + 2\ w_2r_2$	$8\ WwR_2w_2Rr + 8\ WwR_2w_2r_2$ Roan 5, White 6
36.	(WwR_2) (w_2Rr) Roan 5	(WwR_2) (w_2r_2) White 6	$= W_2r_2 + 2\ WwR_2 + w_2R_2$ $= 2\ w_2Rr + 2\ w_2r_2$	$2\ W_2r_2w_2Rr + 2\ W_2r_2w_2r_2 + 4\ WwR_2w_2Rr + 4\ WwR_2w_2r_2$ Roan 8, White 9, Roan 5, White 6 $+ 2\ w_2R_2w_2Rr + 2\ w_2R_2w_2r_2$ Red 2, Roan 3
37.	(WwR_2) (w_2Rr) Roan 5	(w_2R_2) (w_2r_2) Roan 3	$= 2\ WwR_2 + 2\ w_2R_2$ $= 2\ w_2Rr + 2\ w_2r_2$	$4\ WwR_2w_2Rr + 4\ WwR_2w_2r_2 + 4\ w_2R_2w_2Rr + 4\ w_2R_2w_2r_2$ Roan 5, White 6, Red 2, Roan 3
38.	(w_2R_2) (w_2Rr) Red 2	(WwR_2) (w_2r_2) White 6	$= 2\ WwR_2 + 2\ w_2R_2$ $= 2\ w_2Rr + 2\ w_2r_2$	$4\ WwR_2w_2Rr + 4\ WwR_2w_2r_2 + 4\ w_2R_2w_2Rr + 4\ w_2R_2w_2r_2$ Roan 5, White 6, Red 2, Roan 3

TABLE V (*continued*)

	One Parent	2d Parent	Intermediate Calculations	Gametic and Somatic Composition of Offspring
39.	(w_2R_2)	(w_2R_2)	$= 4\ w_2R_2$	$8\ w_2R_2w_2Rr + 8\ w_2R_2w_2r_2$
	(w_2Rr)	(w_2r_2)	$= 2\ w_2Rr + 2\ w_2r_2$	Red 2 Roan 3
	Red 2	Roan 3		
40.	(W_2r_2)	(W_2r_2)	$= 4\ W_2r_2$	$16\ W_2r_2w_2r_2$
	(w_2r_2)	(w_2r_2)	$= 4\ w_2r_2$	White 9
	White 9	White 9		
41.	(W_2r_2)	(WwR_2)	$= 2\ W_2r_2 + 2\ WwR_2$	$8\ W_2r_2w_2r_2 + 8\ WwR_2w_2r_2$
	(w_2r_2)	(w_2r_2)	$= 4\ w_2r_2$	White 9 White 6
	White 9	White 6		
42.	(W_2r_2)	(w_2R_2)	$= 4\ WwR_2$	$16\ WwR_2w_2r_2$
	(w_2r_2)	(w_2r_2)	$= 4\ w_2r_2$	White 6
	White 9	Roan 3		
43.	(WwR_2)	(WwR_2)	$= W_2r_2 + 2\ WwR_2 + w_2R_2$	$4\ W_2r_2w_2r_2 + 8\ WwR_2w_2r_2 + 4\ w_2R_2w_2r_2$
	(w_2r_2)	(w_2r_2)	$= 4\ w_2r_2$	White 9 White 6 Roan 3
	White 6	White 6		
44.	(WwR_2)	(w_2R_2)	$= 2\ WwR_2 + 2w_2R_2$	$8\ WwR_2w_2r_2 + 8\ w_2R_2w_2r_2$
	(w_2r_2)	(w_2r_2)	$= 4\ w_2r_2$	White 6 Roan 3
	White 6	Roan 3		
45.	(w_2R_2)	(w_2R_2)	$= 4\ w_2Rr$	$16\ w_2R_2w_2r_2$
	(w_2r_2)	(w_2r_2)	$= 4\ w_2r_2$	Roan 3
	Roan 3	Roan 3		

when mated with red cows only roan calves are expected if the mating be like mating No. 20; 50 per cent. red and 50 per cent. roan if like No. 23; 50 per cent. roan and 50 per cent. white if like No. 35; and 50 per cent. roan, 25 per cent. red and 25 per cent. white if like No. 38. There is ample explanation for throwing a white calf from a roan cow and a white bull. If the mating be like Nos. 31,

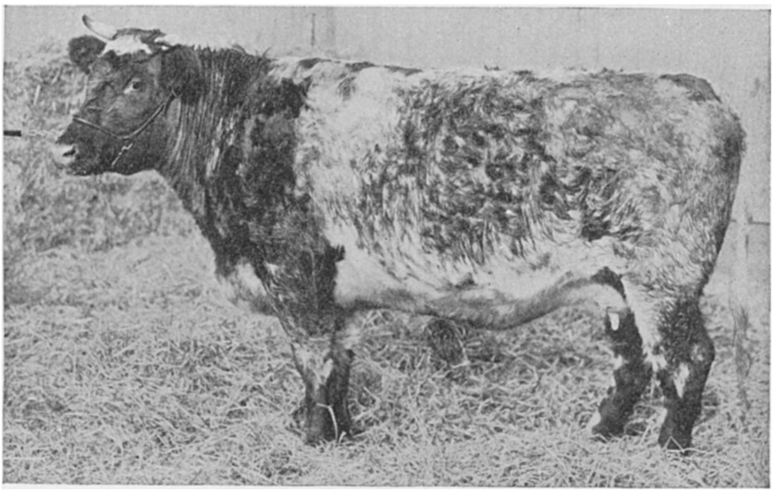


FIG. 4. FLORINDA SULTANA.

FLORINDA SULTANA 70519. *Roan.*

Courtesy of F. W. Harding, Waukesha, Wis.

Dam—Gertrude, Vol. 60, p. 1110. *Red.*	Sire—White Hall Sultan 163573. *White.*
Dam's Dam—Wild Eye Belle 15th. *Red.*	Sire's Dam—Bapton Pearl. *Roan.*
Dam's Sire—Judge Wardell 144980. *Red.*	Sire's Sire—Bapton Sultan 163570. *Roan.*

32, 33 or 44 the chance for roan and white colors are equal; if like No. 36 the ratio of white to roan to red expected is 6 to 8 to 2, but if the mating be of type 42 only white calves can be expected.

Mr. Bruce's array of data concerning the Sittyton cattle presents a very telling table of facts. All possible color matings are made, and in most cases the number of offspring is quite large enough to insure a proportional distribution among the expected colors. The facts of this table fit the hypothesis quite significantly. Of special

interest are the roan by roan matings, which produced 56 reds, 193 mixed color (*i. e.,* roan and red-and-white) and 60 white offspring. This does not fit well into the now abandoned hypothesis that "roans are simplex, reds are duplex and whites nulliplex." The number being quite large should approximate more nearly the expected 50 per cent. of roans, or even less than 50 per cent., inasmuch as some reds were later thought to be simplex; however, there are 62.46 per cent. roans. This may mean that some roans are pure and when mated to like animals will produce only roans—as mating No. 1, wherein two roans produce only roans, which in turn are pure and will reproduce themselves. As further explanation in accounting for an excess of roans—which is common in most herds—note that in matings Nos. 1, 2, 7, 8, 9, 19 and 45 a roan mated with a roan produces roans only. As to the red by red matings, types Nos. 6 and 15 will give only red offspring, while type 30 gives 75 per cent. red and 25 per cent. roan, which fits very well the distribution—133 red, 12 red-and-white, 34 roan and 1 white—with the exception of the one white which will be discussed a little further on. As a matter of fact, every possible color mating has been reported to throw every other color characteristic of the breed.

The red Shorthorn calf of white parentage is no doubt derived as follows: Save for occasional insignificant red patches in the ears, many Park Cattle are *solid* dominant white; this element in a few cattle of the Shorthorn breed would in the course of time, by the laws of chance, make the mating Sets 1 and 2 (WwR_2), Sets 1 and 2 (WwR_2), which would throw 25 per cent. red calves; this apparently is exactly what has happened. Moreover, the much more frequently possible white by white mating

$$\begin{array}{c}(WwR_2)\\ \text{Sets 1 and 2}\end{array}\left\{\begin{array}{c}(WwR_2)\\ \text{Set 1}\\ (w_2r_2)\\ \text{Set 2}\end{array}\right\}\text{ will produce } 12\tfrac{1}{2} \text{ per cent. red offspring.}$$

The red-by-red mating that produces a white calf is

either of *very* rare occurrence or does not occur at all. Besides the cases just referred to, Pearson and Barrington[2] reported two Shorthorn matings reputed to have been red by red that produced white calves. Cases of such rarity and import should be supported by more painstakingly minute evidence than that offered by the

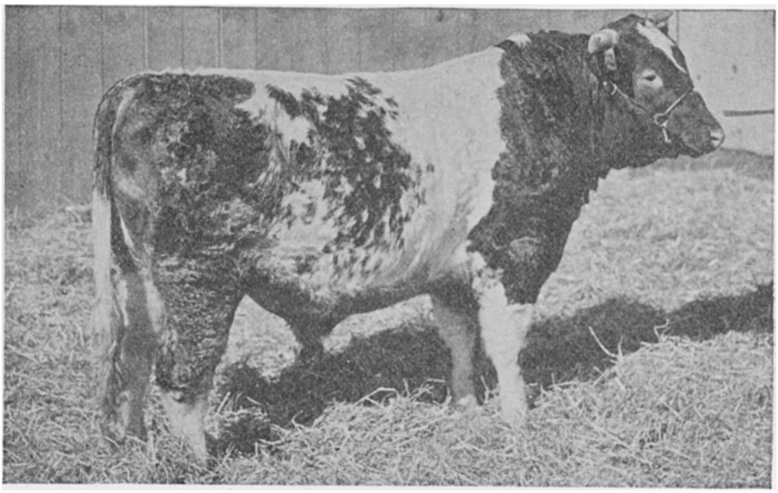


FIG. 5. SPICY SULTAN.

SPICY SULTAN 334972. *Roan.*

Courtesy of F. W. Harding, Waukesha, Wis.

Dam—Spicy of Edna, Vol. 50, p. 532. *Red, little White.*
Dam's Dam—Spicy of Browndale 9th. *Red.*
Dam's Sire—Orange Victor 138562. *Red.*

Sire—Whitehall Sultan 163573. *White.*
Sire's Dam—Bapton Pearl. *Roan.*
Sire's Sire—Bapton Sultan 163570. *Roan.*

herd book, which often records an animal as red though it may have white or roan areas of quite noticeable extent, or an animal as "white" that may have, besides the generally characteristic red in and about the ears, small body areas of red or of roan. Mr. E. M. Hall, a prominent Shorthorn breeder of Carthage, Missouri, in response to a recent inquiry, wrote: "I now, March 30, 1911, have one white calf—from red dam and sire, but it is an inbred calf." In response to further solicitation he

[2] "On the Inheritance of Coat-Colour in Cattle," *Biometrika*, 1905–6, p. 442.

kindly supplied the data for the following descriptive pedigree:

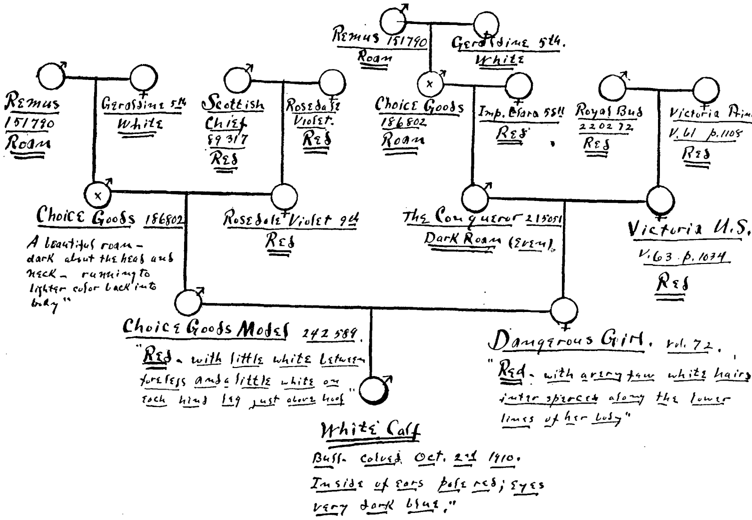


CHART I. Ancestry of White Calf.

Following the nomenclature of this paper this mating, because each parent had both red and white hairs, would be classed as "roan" by "roan" and the white calf could be accounted for easily; but the case should not be dismissed so summarily. There are red Shorthorns without a single white hair and, although red hair in and about the ear is quite persistent, there are *white* Shorthorns without a single red hair. If a mating of such red animals should have been known to have produced a *white* calf it might be accounted for on the grounds of mutation due to an intrusion *de novo* of an inhibitory or destroying antibody in quantity sufficient to affect the entire coat. As an alternative possibility, it might be that by chance the duplex red areas (w_2R_2) of one parent were in the homologous areas of the other simplex red (w_2R_r), a condition very remotely, if at all, possible on account of the absence of the reciprocally colored patterns in cattle. However, should it be possible, the process would be as follows:

	1st Parent	2d Parent		Offspring
Set 1.	(w_2R_2)	(w_2Rr)	$= 2\ w_2R_2 + 2\ w_2Rr$	4 $w_2R_2w_2R_2$ (Red)
Set 2.	(w_2Rr)	(w_2R_2)	$= 2\ w_2R_2 + 2\ w_2Rr$	4 $w_2R_2w_2Rr$ (Red)
	(Red)	(Red)		4 $w_2Rrw_2R_2$ (Red)
				4 w_2Rrw_2Rr (Red)

Now mate two of the latter type—$w_2Rr\ w_2Rr$

			$w_2R_2w_2R_2$ (Red)
			2 $w_2R_2w_2Rr$ (Red)
			$w_2R_2w_2r_2$ (Roan)
			2 $w_2Rrw_2R_2$ (Red)
(w_2Rr)	(w_2Rr)	$= w_2R_2 + 2\ w_2Rr + w_2r_2$	4 w_2Rrw_2Rr (Red)
(w_2Rr)	(w_2Rr)	$= w_2R_2 + 2\ w_2Rr + w_2r_2$	2 $w_2Rrw_2r_2$ (Roan)
			$w_2r_2w_2R_2$ (Roan)
			2 $w_2r_2w_2Rr$ (Roan)
			$w_2r_2w_2r_2$ (*White*)

A white thus derived from two reds would be an albino as far as coat color is concerned. As still another possibility it may be that a strain albinic as to its entire coat entered into the Shorthorn make-up; this, while the simplest explanation, can not, however, be shown historically. While the areas of dominant white and albinic are quite specific, still, in view of the facts that the whitening process is systematically progressive and that the albinic condition is the more advanced, the areas of albinic white must ultimately encroach upon those of dominant white. Thus an animal whose coat is mostly albinic white, bred to a duplex red, would produce a simplex red (with little white), which latter animal could produce white offspring. This may be what sometimes happens. But again it involves the existence of a strain with an entire albinic coat. Thus the behavior in heredity of the pattern and pigments of the white calf belonging to Mr. Hall becomes of absorbing interest. If it should be retained as a herd bull and proves to be an animal of type No. 6 or No. 9, then the "roan-by-roan" theory or the intrusion de novo theory must be accepted; if, however, it will produce black calves when bred to an Angus or Galloway cow "the reciprocal areas" theory or the "albino" theory must be accepted. Present evidence seems to point toward the "roan-by-roan" theory and the impossibility of a mating of an absolutely red by an absolutely red producing any-

thing but red or roan calves—mutations excepted. In the present light, the absence of white calves from red parents, the absence of entire coat albinos, and the absence of theoretical type No. 3 are mutually corroborative phenomena. The fact that white by white—Table I—produced a roan may mean nothing more than that the mating was of type No. 43, in which 75 per cent. white and 25 per cent. roan offspring are expected.

As to the spotted animals, they seem to be of the same nature as the roans. Just as there are mulattos and "spotted" negroes due, respectively, to fine and coarse mosaics of the pigment granules, there are roan cattle, which roan effect is due to a very close intermingling of red and white hairs; and spotted cattle, due to a coarser mosaic of the same, which coarser mosaic came from a distinct inheritance source—doubtless the Dutch bulls of eighteenth century importation, as previously stated. In this paper, the spotted animals have thus far been treated as roans; they have never been popular with breeders, consequently, there are relatively few of them—the few (three) Sittyton matings being typical. It is observed from the table that when a mixed color animal is mated, the mixed color offspring tend to be like the mixed color parent—*i. e.*, either largely roan or largely spotted, as the case may be.

TABLE VI

(Calculated from Table I)

Red by spotted gives	23.3 per cent. spotted	and	12.7 per cent. roan.
Red by roan gives	4.4 per cent. spotted	and	46.6 per cent. roan.
Roan by spotted gives	25.5 per cent. spotted	and	45.3 per cent. roan.

The persistence of spottedness in the offspring of spotted parents is accounted for by the fact that the color areas are definite in location and contour and, being independently transmitted, the registering of fortuitously the red or the white phases of the homologous areas of the two spotted parents will generally produce spottedness in offspring. A similar registering of roan and spotted coats would make the spottedness less pronounced.

There are all degrees of the roan condition, varying from

nearly white to nearly red; this may mean that the set of dominant white hairs and the set of recessive white hairs are not each governed by a single determiner, but by a group of either many or few similarly behaving and generally, but not essentially, synchronously moving determiners. This is consistent with the observed fact that all matings into which roans enter produce more roans than any other color. Thus it appears that, as with spottedness, the degree of roanness is the somatic effect of the fortuitous registering—generally in accordance with the theory of the pure gamete—of the many units composing each of the two independently behaving sets of hairs; this, together with the occasional intra-zygotic inhibition and reaction in response to set conditions, quite completely explains the observed facts. Thus the registering of pigments and patterns may give a measurable somatic

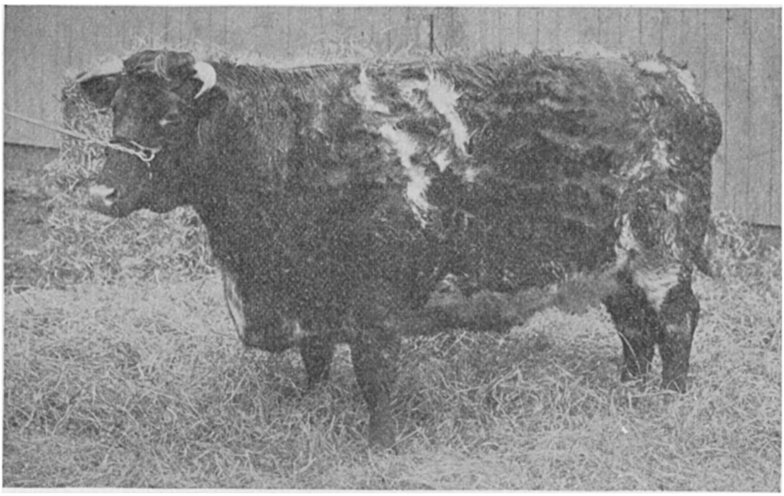


FIG. 6. ROAN LILY.

ROAN LILY 59531. *Roan.*

Courtesy of F. W. Harding, Waukesha, Wis.

Dam—May Lily 59528. *Red.*
Dam's Dam—Mourey May 59529. *Red.*
Dam's Sire—King of Banff (Imp.) 306221. *Roan.*

Sire—Gloster's Choice 284895. *Roan.*
Sire's Dam—Gloster Girl. *Red.*
Sire's Sire—Choice of the Ring 187237. *Roan.*

effect in inheritance without a specific chemical unit determiner for such effect, and the spotted and roan Shorthorns are not blends in the old sense of the term.

Angus cattle which are black sometimes throw dark red colors, exemplifying the fact that in cattle, as with animal pigments generally, the darker pigments are epistatically dominant over the lighter, hence the cattle colors—black, red, yellow with its variations—are dominant over "albinic" white (w), like the white of the Silkie Fowl, but "positive" white (W), like the white of the Leghorn Fowl and such as that of the British Park cattle, is dominant over any and all pigments. Corroborative of this, recall the instance reported by Prof. Wentworth, wherein pure-bred Holstein cows were bred to a deep red Shorthorn bull, and in the offspring "the color pattern showed no trace whatever of the Shorthorn parentage." Now conceive the white Shorthorn coat to be made up of an admixture of "albinic" and "positive" whites, and let the duplex red be mated with the white of this nature—the offspring are the familiar roans, for the "positive" white persists and the "albinic" white is covered by the red pigment. In explanation of the black cattle crosses: Mate a white Shorthorn of type No. 9, or a roan of type 7 or 8, with a black Angus or Galloway; the dominant white persists, the black covers the red (as in human hair) and the familiar blue-roan hybrid results in exact accordance with the theory of gametic purity. Conceive of the white-faced Hereford mated with the black Angus—the "positive" white persists, the black pigment covers the red and the familiar white-faced, black-bodied hybrid results. Thus it is determined that the white of the areas of the face, the two flank belts and the underline are largely "dominant white," while those of the neck, barrel and quarters are mostly "albinic white."

The old single-unit coat hypothesis, even when amended to permit the simplex condition in some reds and in some whites, does not explain *how* the simplex condition could run the *entire* color gamut; neither has the "first generation blend, later generation segregation" theory yet been

reconciled with gametic purity. The old hypothesis is, therefore, abandoned. The facts demand the companion-trait or unit-complex hypothesis modified to permit of occasional intra-zygotic reactions in response to a definite set of conditions, instead of the single-unit notion, and the 45 case matings instead of the typical 6.

The following table is compiled from data reported in *Biometrika,* 1905, 1906,[3] by Amy Barrington and Karl Pearson from Coates's Shorthorn Herd Book.

TABLE VII

Mating	Offspring						
	Red	Red little White	Roan	Spotted	Total Mixed	White	Total
1. Red by red	156	23	6	11	40	0	196
2. Red by roan	243	46	324	39	409	4	656
3. Red by white	1	2	85	2	89	0	90
4. Roan by roan	104	43	286	69	398	84	586
5. Roan by white	1	1	47	1	49	24	74
6. White by white	0	0	0	0	0	3	3

In addition to this, special search[4] for white-by-white matings yielded 91 cases, giving 1 red, 4 roan and 86 white offspring; in two cases, red-by-red matings were reported to have given white offspring.

The color distribution of this table practically parallels that found in the Cruikshank herd as reported by Mr. Bruce and that of the other compilations herein recorded.

Barrington and Pearson then proceeded with the following criticism:

> . . . No simple Mendelian formula applies rigidly. We find ourselves neglecting sensible percentages of occurrences incompatible with the theory of the pure gamete.[5]

It is true that the first studies in color in Shorthorn cattle suggested the single-unit color coat hypothesis and as late as 1909 James Wilson, of the Royal College of Dublin, in his interesting book on the "Evolution of British Cattle," suggested this hypothesis. It is not, however, the sole possible Mendelian interpretation, but rather the

[3] *Ibid.,* pp. 427–464.
[4] *Ibid.,* p. 441.
[5] *Ibid.,* p. 454.

preliminary working analysis. The "sensible percentages" that Pearson objects to also impel the most ardent adherent of the pure gamete theory to discard the single-unit color coat hypothesis and to seek the unit—however great or small—that does behave in the expected fashion. We must agree with the above criticism that the incompatible percentages and the exceptions are too persistent to ignore; such percentages simply indicate that the

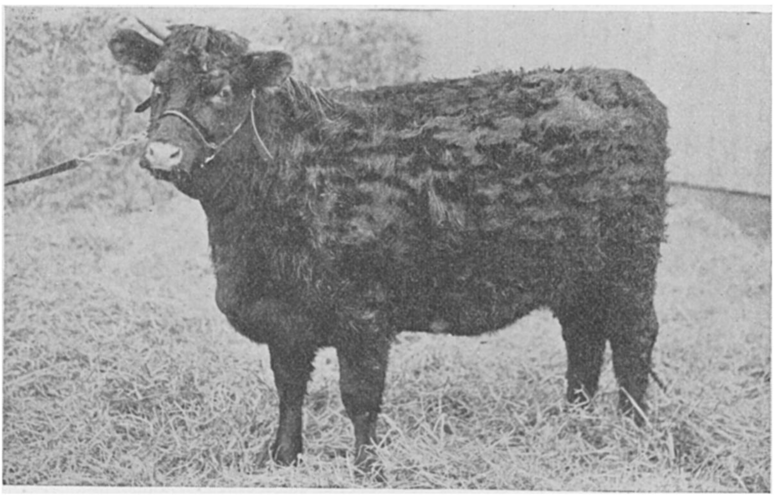


FIG. 7. RED LADY 6TH.

RED LADY 6TH 86626. *Red.*

Courtesy of F. W. Harding, Waukesha, Wis.

Dam—Red Lady (Imp.). *Red, little White.*
Dam's Dam—Roan Mary. *Roan.*
Dam's Sire—Cornelius 226511. *Red.*

Sire—Baron Sultan 300788. *Red and White.*
Sire's Dam—Athene of Riverdale. *Red.*
Sire's Sire—Whitehall Sultan 163573. *White.*

ultimate unit, or unit-behaving group of characters, is not isolated, and that besides gametic segregation there is occasionally intra-zygotic reaction. The old hypothesis then must be abandoned and another better fitting the facts must be worked out. Among other things the behavior of the unit complex must be studied. Thus, if a Shorthorn is crossed with an Angus, the pure gamete theory does not lead us to expect a series of "blends" or of one of the pure parental types in the F_1 generation and

25 per cent. pure Shorthorn, 50 per cent. blends and 25 per cent. pure Angus in the F_2 generation. If all the independent units moved with absolute synchronism this would be expected, but they are genetically independent and the laws of chance demand that the greater the number of units the more intricate becomes the task of extracting an animal with the combination of a great number of arbitrarily selected traits such as compose any of the pure breeds of domestic animals.

Barrington and Pearson in referring to the blue-gray hybrid and white Shorthorn cross give evidence showing that sometimes blue-gray, sometimes "grizzled" and sometimes white animals result.[6] Quoting Mr. Hodgson, they say: "This cross gives white cattle which are not, however, to be reckoned as pure white Shorthorns."[7] If all the characters essential to differentiating "pure-bred" Galloway and "pure bred" Shorthorn cattle from each other were reduced to their ultimate inheritable units, the laws of chance having free play, we should expect in F_2 one "pure-bred" Shorthorn and one "pure-bred" Angus in 4^n individuals—in which n is the number of ultimate units. A conservative estimate would certainly make this number at least a score, but more likely a hundred or a thousand. Taking into consideration the fact that the phases of the units patent in Shorthorn and Angus cattle are not uniformly dominant or recessive, that the same units that distinguish Shorthorns from cattle in general may not also distinguish Angus from cattle in general, it is obvious that the chance of producing a "pure" animal in F_2 from such a combination is very remote. Thus, if the differentiating traits be uniformly dominant or recessive and only ten in number, the chance of securing such a combination would be one in 1,048,576. The close and exceptional fitting of many cases to the simply four-part Mendelian ratio is the only conclusive evidence of the location of the ultimate unit. It is infinitely easier to approximate one of the

[6] *Ibid.*, p. 433.
[7] *Ibid.*, p. 433.

parental types by breeding back to the desired type—the "pure sire" method— than to extract it from F_2 hybrids by the operation of the laws of chance. In the general run of cattle the 7/8 grades are quite like the pure types; 15/16 grades are much more so, while 31/32 or 63/64 are generally so like the pure breed as to be, except for arbitrary rules, eligible for registration. All of which tends to support the pure gamete theory, in that under such a process the laws of chance rapidly "quarter out" the foreign units, albeit rigid selection can, of course, as it often does, maintain any one of the mongrel types indefinitely. If the number be great, the longer the process and the more likelihood of "reversion." The theory of the pure gamete is not inconsistent with the somatic blend in F_1; in fact, it demands it in the coarser aspects. Such a blend indicates that a unit complex rather than a single unit is under observation.

All the data so admirably collected by Barrington and Pearson yield most readily to a Mendelian interpretation, if by such interpretation is meant the purity, segregation and fortuitous recombination of the unaltered determiners of unit characters, provided such interpretation is not held to be inconsistent with frequent intra-zygotic reactions between the determiner and some antibody occasioned by the definite relative concentration and intimacy of the two bodies. They reject a Mendelian interpretation on the grounds that the whole coat does not behave as a single unit. Gametic purity of the unit character might as well be rejected on the grounds that the whole animal with its thousands of characters does not so behave, or that there are occasional intra-zygotic reactions causing mutations. In mentioning the types of cattle going into the making of the Shorthorn, they continue:

> Upon the ingredients just referred to, the breeders had to work when pedigree cattle breeding, which is scarcely more than a century old, came into vogue. The Shorthorn had possibly arisen from four races: the Celtic, a Romano-British, an Anglo-Saxon and the "Dutch" and even some of these are mixtures. . . . Thus the Shorthorn Red may

have had three sources—an Anglo-Saxon red, the red of the Dutch flecking, and the supposed Celtic red. The white may have come through the Romano-British, through the Anglo-Saxon white or possibly through the white in the Dutch. The particolors and the roans are of equally doubtful origin, although it probably is safe to assert that they are due to the breeds of latest importation; and it thus seems fairly impossible to determine *a priori* how many distinct red, roan, particolor or white types may really exist in the case of the Shorthorn. The importance of this statement for any Mendelian interpretation must be obvious. We may have reds which are dominant, recessive or even heterozygous to white or even to other reds, and the search for a Mendelian formula becomes very elusive. . . . We have seen that there is historically a possibility of two strains of red and two strains of white having been mingled in the Shorthorn. Determinants representing particolor and white markings can undoubtedly be introduced also; we confess to having made an attempt from this standpoint which shattered with further examination of Table I.—but the introduction needs a wider practise than we can boast of in inventing Mendelian formulæ and until we are more convinced than we are at present of the soundness of such formulæ we should prefer to leave the invention to those who have had it. Coates Herd Book presents a wide range of material and whatever we may think of the categories selected, the record has been made by persons in absolute ignorance of recent controversies about heredity. It is therefore really impartial material for Mendelians to unravel. . . . It would thus seem that no simple Mendelian formula can possibly fit the Shorthorn cases. Roughly, such a formula approaches the data in one or two points but the roughness appears inconsistent with a theory of Mendelism being due to the purity of gametes. It is of course clear that the introduction of a complex allelomorph may improve matters, or the differentiation of whites and reds into different classes, homozygous and heterozygous. Increase in the number of available variables usually does give better fits.[8]

The whole color problem in Shorthorns is a complicated study in mongrelism and no single simple four-part Mendelian ratio can be expected to explain it. Instead of a single unit or a single uniformly dominant or recessive series, there are two genetically independent unit-behaving groups of units—one dominant, the other recessive in their companion, *i. e.*, their white phases. However, such companion traits—if the somatic blend is considered as simplex—when undistinguished, will give the

[8] *Ibid.*, p. 444.

simple four-part Mendelian ratios in 42 case matings out of 45, the exceptions being matings 28, 29 and 36. In summing up the coat-color inheritance of blue-gray cattle, Barrington and Pearson say on page 435, "It will need a complex allelomorph to describe these color changes, if, indeed they can be described at all." With this it must be agreed. The "complex" allelomorph is, however, not so complex, after all; the complex is simply a group of

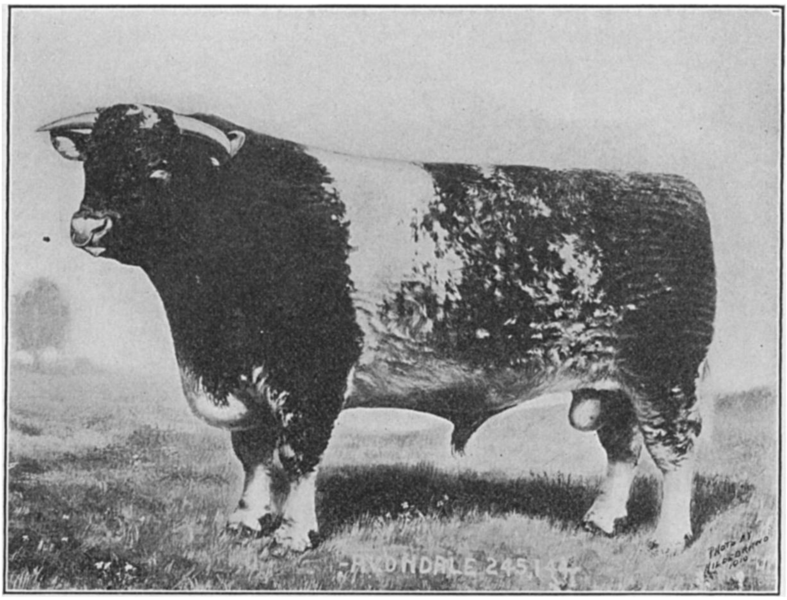


FIG. 8. AVONDALE.

similar units each independently transmitted. If they were less uniform in their somatic aspects they would not be so confused. The task of segregating the unit becomes more difficult but not at all impossible.

Barrington and Pearson emphasize the statement that the evidence of the breeders of the blue-grays is that a white Shorthorn bull of white parentage is greatly to be preferred to one of roan parentage, inasmuch as the former type invariably gives the desired blue-gray color —referring to Mr. deVere Irving:

AVONDALE 245144. *Roan.*

Courtesy of Carpenter and Ross, Mansfield, Ohio.

Avondale *Roan* 245144 Jan. 5, 1905 E. S. Kelly Yellow Springs, Ohio	White Hall Sultan *White* 163573 J. Deane Willis	Bapton Sultan *Roan* 163570 J. D. Willis	Bapton Victor *Roan* 163571 J. D. Willis	Count Victor 132574 *Roan* J. D. Willis
				Cowslip Vol. 41 p. 678 E. *Red* J. D. Willis
			Moon Daisy *Red* Vol. 42, p. 704 E. J. D. Willis	Captain of the Guard 132059 Red A. Cruickshank
				Wiltshire Daisy *Red and White* J. D. Willis
		Imp. Bapton Pearl *Roan* Vol. 48, p. 368 J. D. Willis	Count Lavender *Roan* 132575 W. Duthie	Norseman 132576 *Red* A. Cruickshank
				Sweet Lavender Vol. 33, p. 307 E. *Roan* W. Duthie
			Primrose 2d *Roan* Vol. 39, p. 228 E. W. Duthie	Golden Crown 157369 *Roan* A. Cruickshank
				Primrose *White* A. Davidson
	Imp. Avalanche 2d *Roan* Vol. 60, p. 655 C. H. Jolliffe	Mescombe *Red, little White* 222700 S. H. Allen	Captain Lavender *Red* 222673 J. D. Willis	Captain of the Guard 132059 *Red* A. Cruickshank
				Lavender 58th *Roan* A. Cruickshank
			Meadow Pipit 7th *Red* S. H. Allen	Kinsman 53d 222691 *Red, little White* R. Wood
				Meadow Pipit 4th *Red, little White* S. H. Allen
		Avalanche *Roan* Vol. 45, p. 786 E. W. A. Mitchell	Sittyton Scarlet *Red* 151407 A. Cruickshank	Cumberland 50626 *Roan* A. Cruickshank
				Amaranth Vol. 34, p. 308 E. *Red* A. Cruickshank
			Averne 10th *Roan* J. Bruce	Snowball 140037 *White* J. Bruce
				Averne 6th *Red* J. Bruce

He finds on using a white bull of roan parentage that the offspring are liable to come dark, some almost black, in color and others very dark blue-gray.[9]

No better material for Mendelian interpretation than this could be offered. It simply means that the white bull of "white parentage" is more likely to be of type "9" (a roan bull of type 7 or 8 would do as well); the whole becomes a mating of type No. 20, which expects 100 per cent. roans—black taking the place of red the

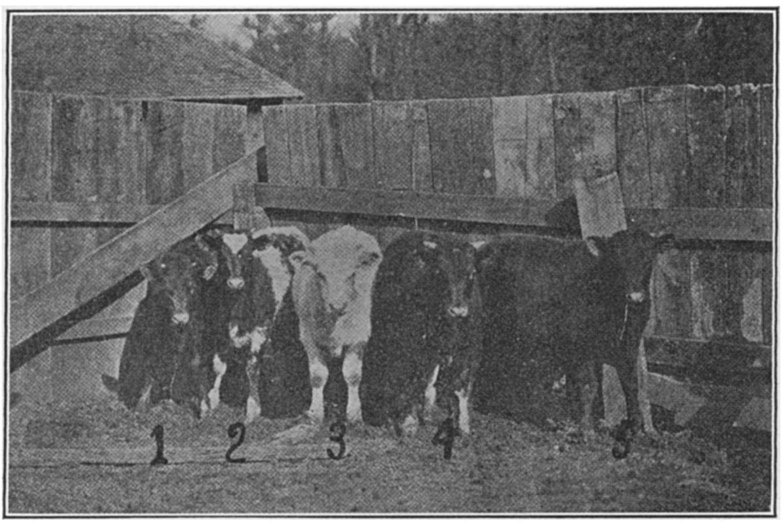


FIG. 9. AVONDALE'S FIRST CALVES.

roan becomes blue-roan or "blue-gray." A white bull of "roan parentage" is more likely to be of type "6" (a roan of type 4 or 5 would do as well—see matings Nos. 5 and 14), which mated to a pure black would produce 50 per cent. blue-roans and 50 per cent. blacks, in accordance with a mating of type No. 23. Wild white cattle which occasionally drop red or black calves, when crossed with a white Shorthorn produce white offspring. Such a female offspring when bred to a white Shorthorn bull "may produce a considerable percentage of both roan and red as well as of white calves."[10]

[9] *Ibid.*, p. 432.
[10] *Ibid.*, p. 442.

AVONDALE'S FIRST CALVES

Courtesy of Carpenter and Ross, Mansfield, Ohio.

Sire—Avondale. ROAN.
Sire's Dam—Imp. Avalanche 2d. *Roan.*
Sire's Sire—Whitehall Sultan. *White.*
Sire's Dam's Dam—Avalanche. *Roan.*

Sire's Dam's Sire—Mescombe. *Red, little White.*
Sire's Sire's Dam—Imp. Bapton Pearl. *Roan.*

Sire's Sire's Sire—Bapton Sultan. *Roan.*

Calf No. I. Colonel. *Dark Roan.*
Dam—Chrysanthemum. ROAN.
Dam's Dam—Christina. *Roan.*
Dam's Sire—General White. *White.*

Calf No. II. Max Rosewood. *Roan.*
Dam—Rosewood 86. ROAN.
Dam's Dam—Rosewood 81. *Roan.*
Dam's Sire—Pride of Day. *Roan.*

Calf No. III. Wall Street. *White.*
Dam—Wedding Gift 16. ROAN.
Dam's Dam—Wedding Gift 12. *Roan.*
Dam's Sire—Royal Prince. *Roan.*

Calf No. IV. Sir Collin Campbell. *Red, little White.*
Dam—Ury Lassie. RED, LITTLE WHITE.
Dam's Dam—Ury of Greenwood. *Red, little White.*
Dam's Sire—Royal James. *Red.*

Calf No. V. Max Clipper. *Red.*
Dam—Miss Council. ROAN.
Dam's Dam—Christina. *Roan.*
Dam's Sire—Council. *Roan.*

Precisely this phenomenon was paralleled experimentally and given a clear Mendelian explanation by Davenport,[11] who mated the dominant white of the Leghorn fowl with the recessive white of the Silkie. The F_1 generation, save for some red on the wings of the males, was white; this F_1 generation mated *inter se* gave some individuals with the typical ancestral Jungle fowl coloration. The fact that the Park cattle generally breed white but occasionally throw a red or a black calf means that generally the germ cell formula is (W_2R_2), which will throw all white, but sometimes is (W_wR_2), a strain of which introduced into a breed will throw the "occasional red calf." The introduction of a strain of partial albinism seems to effect this cleavage and apparently is brought about as follows:

[11] "New Views about Reversion," *Proceedings of the American Philosophical Society,* Vol. XLIX, No. 196, p. 294.

	Offspring			
Wild White Cow	1	2		
Body areas 1 and 2	$8\ WwR_2$	$WwRr$	*White*	F_1 100 per cent. White.
Germ cells W_2R_2	$8\ W_2R_2$	$WwRr$	*White*	
White Shorthorn Bull No. 6				
Body areas 1 2				
Germ cells WwR_2 w_2r_2				
1 2				
$2\ W_2R_2 + 2\ WwR_2$ $4\ WwRr$				

Now mate a female of one of these types—*e. g.*, $1/W_wR_2$ $2/W_wR_r$ with a white Shorthorn bull—*e. g.*, one of type No. 6.

Areas	1	2
Hybrid cow	WwR_2	$WwRr$
Bull No. 6	WwR_2	w_2r_2
	1	2
	$W_2R_2 + 2\ WwR_2 + w_2R_2$	$WwRr + w_2r_2 + Wwr_2 + w_2Rr$

1	2	
W_2R_2	$WwRr$	*White*
W_2R_2	w_2r_2	*White*
W_2R_2	Wwr_2	*White*
W_2R_2	w_2Rr	*Roan*
$2\ WwR_2$	$WwRr$	*White*
$2\ WwR_2$	w_2r_2	*White*
$2\ WwR_2$	Wwr_2	*White*
$2\ WwR_2$	w_2Rr	*Roan*
w_2R_2	$WwRr$	*Roan*
w_2R_2	w_2r_2	*Roan*
w_2R_2	Wwr_2	*Roan*
w_2R_2	w_2Rr	*Red*

No theory not involving the purity—*i. e.*, chemical identity, of the determiner and its segregation and recombination in unaltered form, together with occasional intrazygotic inhibition and reaction in response to specific conditions, can explain the facts reported by Barrington and Pearson, which facts of observation tally with those reported from many other sources.

Confirmatory of the declaration that the white of the wild Park cattle is dominant white, the following evidence by Storer—referring to the Chartley cattle—is offered:

> Whatever cows were put to the white bulls, the calves came almost invariably the color of their sires; the only instance he remembered to the contrary being that on one occasion a dark-colored cow produced a spotted calf. Thus were singularly confirmed at Chartley two of the facts which Bewick relates with regard to Chillingham—the existence of the custom and the prepotency of the white sire.[12]

[12] "The Wild White Cattle of Great Britain," p. 239.

And further, in quoting Mr. John Thornton he says:

> The peculiarity most striking was the color; a clear white body, head and neck, with much hair; but the ears, nose, circle around the eyes, and the hoofs were black, and there were a few black spots on the fetlock above the hoof.[13] Black calves are not at all uncommon. . . . When the variation of color occurs the calves are always pure black, "with not a white hair on them" never particolored. . . .[14]

Professor S. Cossar Ewart, of Edinburgh, writes (April 11, 1911):

> Some years ago I saw at Chillingham crosses between these white Park cattle and white Shorthorns—all the crosses were white or light cream color.

Recently under his direction wild Chartley bulls were crossed with domestic heifers. The matings and offspring are indicated by chart No. 2, which was drawn from data supplied by him.

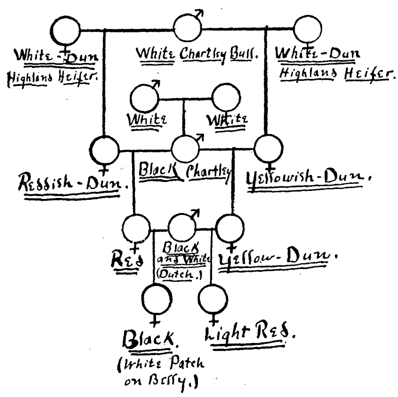


CHART II. Ewart's Experiment.

From this, as from other pedigrees, it appears that the white of the Park cattle is dominant white, that, barring dominant white, the darker pigments are epistatically dominant over the lighter ones, but that neither dominancy and segregation nor the coexistence of several pigments, nor midway blends—all of which may operate here—entirely explains the facts; there must also be occasional intra-zygotic reaction and mutations.

[13] *Ibid.*, p. 241.

[14] *Ibid.*, p. 237.

The behavior of the crest when a crested fowl is mated with a non-crested variety is typical of the behavior of somatic blends tending to obscure gametic segregation. Davenport[15] has shown that there are two genetically independent factors united in the crest: One, erectness of feather growth over a certain area is *dominant* over the normal condition; the other a continued growth of feathers of this area is *recessive* to the normal growth. Hence, in the F_1 generation there is an apparent "blend," the feathers being short but erect. From F_1, however, in subsequent generations, Davenport has extracted a beautiful complete crest. There are many other striking somatic blends—among them the case of the Andalusian fowl, of the human mulatto, and of the human hermaphrodite. Blends are essentially the somatic aspects of the fortuitous combinations of the patent and latent phases of two or more genetically independent units. In this sense Galton's law may justly stand for the general measure of ancestral influence—a measure of the operation of the laws of chance. The existence of somatic blends can not be denied, for they are among the most definite things commonly observed in inheritance. The more cursory the examination and the more general the view of such cases, the more seeming the blend; however, a more minute inspection often reveals the segregation of the parental factors, all of which points towards the minuteness of the unit character and the purity of the gamete. Were blending, in the commonly understood sense a fact, all individuals of a race or a strain would in a few generations become identical with each other. It is the creation of new units by intra-zygotic reactions and intra-gametic intrusions, together with the segregation and recombination of the unaltered ultimate units of inheritance that have given selection such an opportunity for developing so many strains and species.

[15] "Inheritance in Poultry," p. 69.

(To be concluded)